Regeneration of salal (*Gaultheria shallon*) in the central Coast Range forests of Oregon[1]

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Regeneration of salal (*Gaultheria shallon* Pursh.) by seedling establishment and vegetative expansion was examined under various forest conditions in the central Coast Range of Oregon. Size and expansion rate of individual clonal fragments were negatively correlated with overstory stand density ($p \le 0.039$). As overstory basal area increased from 25 to 75 m^2/ha, mean annual growth percentage of clone rhizome systems decreased from 23.7 to 0.0% and mean total rhizome length decreased from 102 to 0.89 m. Interclonal competition in dense clumps of salal apparently causes rhizomes to die and clones to fragment. In these patches, rhizome biomass and density, aerial stem biomass and density, and total biomass were negatively correlated with overstory density ($p \le 0.01$). For example, in clearcuts, salal clumps had up to 177.7 m rhizome/m^2 and 346 stems/m^2, whereas patches under dense overstories had as few as 10.6 m rhizome/m^2 and 19 stems/m^2. Aerial stem populations had uneven-age distributions of aerial stems in all overstory conditions. This structure is apparently maintained through annual production of new ramets. Salal seedling establishment rates were significantly affected by study site location, overstory density, and substrate ($p \le 0.05$). Two-year survival was highest on rotten logs and stumps in thinned stands.

Key words: clonal morphology, clone populations, Douglas-fir forests, *Gaultheria shallon*, seedling establishment, vegetative expansion.

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Les auteurs ont examiné la regénération du salal (*Gaultheria shallon* Pursh.) par établissement de semis et expansion végétative, sous différentes conditions forestières, dans le centre du Coastal Range en Orégon. On observe une corrélation négative ($p \le 0,039$) entre la dimension et le taux d'expansion des fragments de clones individuels et la densité de la couverture arborescente de la station. Lorsque la surface basale de ce couvert passe de 25 à 75 m^2/ha, le pourcentage annuel moyen de croissance des systèmes de rhizomes clonaux diminue de 23,7 à 0,0%, et la longeur totale de rhizome diminue de 102 à 0,89 m. Dans les touffes denses de salal, la compétition interclonale entraine apparemment la mort de rhizomes et la fragmentation des clones. Dans ces touffes, la biomasse et la densité des rhizomes, la biomasse et la densité des tiges aériennes, et la biomasse totale montrent une corrélation ($p \le 0,01$) négative avec la densité de la couverture. Par exemple, dans les coupes à blanc, les touffes de salal développent jusqu'à 177,7 m de rhizome/m^2 et 346 tiges/m^2, alors que sous des couvertures denses elles développent aussi peu que 10,6 m de rhizome/m^2 et 19 tiges/m^2. Sous toutes les conditions de couverture, les populations des tiges aériennes sont inéquiennes. Cette structure est apparemment maintenue par la production annuelle de nouvelles ramètes. Les taux d'établissement des semis du salal sont significativement affectés par la localisation du site d'étude, la densité de la couverture arborescente et le substrat ($p \le 0,05$). Après 2 ans, on retrouve la survie la plus forte sur les troncs et les souches pourries, dans des stations éclaircies.

Mots clés : morphologie clonale, populations clonales, forêts de sapin Douglas, *Gaultheria shallon*, établissement des semis, expansion végétative.

[Traduit par la rédaction]

Introduction

Salal (*Gaultheria shallon* Pursh.) is an evergreen, rhizomatous shrub that is common in the understory of coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) − western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) forests of the Pacific Northwest. It often forms extensive patches that dominate understory plant communities (Long 1977) and compete with commercial tree species for moisture and possibly for nutrients (Black et al. 1980; Price et al. 1986; Vihnanek and Ballard 1988; Weetman et al. 1990). The leaves and fruits of salal are beneficial to wildlife (Van Dersal 1938; Cowan 1945; Martin 1971); its stems are used as greenery by florists (Dimock et al. 1974) and its rhizomatous growth makes it suitable for coastal dune stabilization (Brown and Hafenrichter 1962) and urban landscaping.

To date, little is known about the clonal development of salal or the effects of overstory stand density on the clonal morphology of the species. Most previous research deals primarily or exclusively with aboveground characteristics of salal such as flowering and biomass dynamics of stems and leaves (Sabhasri 1961; Long and Turner 1975; Long 1977; Vales 1986; Messier et al. 1989; Bunnell 1990; Smith 1991). Few studies examined the belowground morphology or clonal characteristics of salal (Sabhasri 1961; Bunnell 1990; Messier and Kimmins 1991; Messier 1992). Knowledge of clonal characteristics is necessary for interpreting plant population behavior and evolution and for gathering clues to competitive strategies (Cook 1983), information that in turn, is important for understanding forest stand dynamics and developing appropriate silvicultural practices.

Past studies of clonal shrubs in coniferous forests indicate that some species may persist and maintain a dense population for many years. For example, Kurmis and Sucoff (1989) found that populations of hazel (*Corylus cornuta* Marsh.) maintained an uneven-age population of aerial stems for 20 years. Total stem number varied during this period, but the distribution of stem ages remained relatively constant as repeatedly produced new stems replaced older ones that died. Clonal populations of

TABLE 1. Description of study sites

	Randall Saddle	Cape Creek	Cascade Head
Latitude (N)	44°25'	44°05'	45°03'
Longitude (W)	123°50'	123°57'	123°59'
Elevation (m)	150–350	100–300	100–300
Annual precipitation (cm)*	178	178	251
Avg. summer temp. (°C)	17	15	15
Avg. winter temp. (°C)	5	9	5
Soils	Moderately well drained; clay loam	Moderately well drained; silty clay loam; acidic	Moderately well drained; silty clay loam; acidic
Dominant overstory species	Pseudotsuga menziesii	Pseudotsuga menziesii – Tsuga heterophylla	Pseudotsuga menziesii – Tsuga heterophylla
Dominant understory species	Gaultheria shallon, Rubus spp., Vaccinium spp., Sambucus callicarpa, Polystichum munitum	Gaultheria shallon, Acer circinatum, Rubus spp., Polystichum munitum	Gaultheria shallon, Vaccinium spp., Rubus spp., Acer circinatum, Sambucus caerulea

*Climate data from NOAA 1987.

salmonberry (*Rubus spectabilis* Pursh.), another coastal Oregon shrub, also apparently maintain a dense cover in a range of overstory conditions by annually recruiting new aerial stems (Tappeiner et al. 1991; Zasada et al. 1992). We hypothesized from field observations and from the work of Bunnell (1990), who found that salal plants under both open and closed canopies produced new shoots, that salal might have a similar strategy.

Knowledge of the conditions necessary for salal seedling recruitment is also limited. Observation of salal seedlings in the field has been rare (Sabhasri 1961), and salal seedling survival was reported as very low relative to that of associated understory species (Tappeiner and Zasada 1993). However, salal seeds were found in forest floor seed banks (McGee 1988) and in laboratory experiments showed no cold stratification requirements and germinated more readily on forest floor substrate than on mineral soil (Dimock et al. 1974; McGee 1988; J.C. Zasada, unpublished data). Studies of other Northwest forest species, such as western hemlock and Sitka spruce (*Picea sitchensis* (Bong.) Carr.) (Christy and Mack 1984; Harmon 1987) also linked substrate type to seedling establishment rates; in particular, they identified "nurse logs" as important regeneration sites. From these various study results and those of a pilot study conducted in 1987–1988 (Huffman 1993), we hypothesized that salal seedling emergence and survival is influenced both by overstory density and by substrate.

Our overall objective in performing the two studies (clone and seedling) reported here was to determine how salal colonizes and maintains itself in the understories of Douglas-fir forests by vegetative and seedling reproduction. In the clone study, we examined the relationship between overstory stand density and (*i*) the development and structure of individual salal clones and (*ii*) the age structure, biomass, and ramet and rhizome density of salal clone populations. In the seedling study, we determined the rates of salal seedling establishment and growth on several substrates (mineral soil, undisturbed forest floor, and logs and stumps) under three classes of overstory (thinned, unthinned, and clearcut).

Methods

Study sites and stand selection

The clone and seedling regeneration studies were both conducted on sites in the *T. heterophylla* vegetation zone (Franklin and Dyrness 1973) of Oregon's central Coast Range. The seedling study was done at two coastal sites, Cape Creek (CP) (44°05'N, 123°57'W) and

Cascade Head (CS) (45°03N, 123°59'W), and at Randall Saddle (RS), which was further inland (44°25'N, 123°50'W). The clone study was done entirely at RS. Although these three sites represented somewhat contrasting environments (Table 1), salal formed a dominant understory in all of them.

The clone study included two components: individual clones and clone populations. For studying individual clones, nine stands at RS, representing a continuum of overstory densities (Table 2), were selected. Because excavation of individual clones was impossible in clearcuts (rhizomes were too densely interwoven), only thinned and unthinned stands were included in this component of the clone study. For studying clone populations, we chose 10 RS stands; this set included unburned clearcuts (Table 2). For the seedling establishment study, stands representing three broad overstory conditions (clearcut, thinned, and unthinned) were selected at each of the three study sites (one of each overstory condition at CS and CP and two of each at RS). Unfortunately, one thinned stand selected at RS was clearcut harvested before the end of the first growing season.

For stands used in the clone study, overstory density values were determined by averaging measurements taken from between one and four 0.04-ha fixed plots, centered on clone (or clone population) excavation sites. Trees within the fixed plots were counted and their diameters were measured at breast height (1.4 m). Reineke's stand density index (SDI) (Reineke 1933), Curtis's relative density (RD) (metric) (Curtis 1982), and basal area (BA) (m²/ha) were calculated for each stand.

For both the clone study and the seedling study, percent sky, an additional stand density measurement, was determined by using a pair of LI-COR LAI-2000 plant canopy analyzers (LI-COR Inc. 1989; Welles 1990; Gower and Norman 1991). This measurement, an estimation of the relative amount of sky not obscured by foliage and branches, was collected at 1.4 m above clone excavation sites and 1 m above seedling plots. The average of 20 readings was used to estimate percent sky in each stand in the clone study; in the seedling study, the average of three readings per seedling plot was used. In the clone study, stand assignment to one of the three broad overstory categories (clearcuts, thinned stands, or unthinned stands) was based on the overstory density calculations. In the seedling study, stand assignment to one of these categories was based on visual estimates.

Sampling techniques

Clone study

For individual clone sampling, we excavated from 3 to 9 clones or clonal fragments per stand (for a total of 51 clones) using hand trowels and small picks. Each excavation started at a ramet that was either invading unoccupied forest floor space or located within a dense patch of older salal stems. All rhizomes and associated aerial stems connected to that ramet were then carefully uncovered until the entire clone or clonal fragment was revealed. We use the term clonal

TABLE 2. Characteristics of Douglas-fir stands used for individual clone and clone population studies

No. of stands	Overstory type	Age (years)	No. trees/ha	BA*	SDI†
Individual clone study					
3	Young unthinned	30–40	1400–2000	35–42	360–400
4	Unthinned	60–80	250–440	50–75	270–375
2	Thinned	60–80	90–165	20–35	140–250
Population study					
3	Clearcut	1–8	800–900	1	1
4	Unthinned	60–80	250–440	50–75	270–375
3	Thinned	60–80	90–165	20–35	140–250

NOTE: All stands were located at Randall Saddle. No individual clones were excavated from clearcuts because rhizome networks were too dense. Only small remnant clones occurred in 30- to 40-year-old unthinned stands, and no dense clumps were found in these stands.
*BA, basal area (M^2/ha).
†Reineke (1933). Maximum SDI for Douglas-fir is 590, i.e., 590 10-inch trees/acre or 1458 25-cm trees/ha.

fragment to refer to all connected rhizome and aerial stems, not the complete genet. Our definition of ramet follows Cook's (1983): one or a group of aerial stems produced basally from buds on rhizomes, which have the potential for independent survival.

For each excavated clone, we measured (i) length of current-year rhizome extensions, (ii) length of rhizome modules from all previous years, (iii) number of ramets per clone, (iv) number of aerial stems per ramet, (v) aerial stem length, and (vi) aerial stem age. Current rhizome extensions were unsuberized, fleshy, and white-pink, and had obvious bud scales; these were measured from the distal growing tip to the point of suberization. Previous rhizome modules were brown-black, well suberized, and generally lacked bud scales. The length of these modules (the product of a single meristem) was measured either from the distal tip to the proximal point of branching or between rhizome branches. Aerial stem growth apparently is influenced by the seasonal abortion of the apical meristems. Thus, the seasonal branch elongation results from lateral shoot expansion. This zigzag pattern of branch elongation enabled us to estimate aerial stem ages by counting seasonal branch growth and cross-referencing against xylem ring counts. In addition, for 13 clones, we mapped the spatial arraignment and density of rhizomes, ramets, and roots, noting branching angle, rhizome depth, and rhizome and aerial stem growth patterns.

Clone populations were sampled on three 1-m² plots per stand. Sampling included measurements of salal stem populations, above-ground biomass, rhizome length, and rhizome biomass. To define the 1-m² plots, wooden frames were randomly placed in dense salal patches that completely covered the forest floor. Aerial stems that originated within the perimeter of the frames were clipped, measured for length, and aged. A subsample of the aerial stems was also measured for length, dried at 70°C for 48 h, and weighed. The forest floor within the frame was removed and all rhizomes to a depth of 50 cm were excavated. The excavated rhizomes were cleaned and measured for total length, and biomass was determined after drying the rhizomes at 70°C for 48 h.

Seedling study

Salal fruits were collected during November 1990 near the Oregon State University campus in Corvallis and near the CS study site. The fruits were dried on wire mesh screens and then ground with a mortar pestle. Seeds were separated from the fruit material with a fine sieve and were then stored at 7°C until sowing.

In December 1990 the collected seeds (about 400 per plot) were sown in 30 circular plots, 0.5 m in diameter, in each stand. The 30 plots were divided evenly among three substrate types: (i) rotten logs or stumps of decay class III or IV (Sollis 1982); (ii) mineral soil where we removed forest litter and vegetation; and (iii) undisturbed forest floor. Within each substrate type, the plots were randomly located. The seedling plots were monitored monthly from March 1991 to September 1992 by counting seedlings and noting mortality. Heights of the tallest seedlings were recorded at the end of the first growing season, and up to 50 seedlings per stand were randomly measured for height at the end of the second growing season.

To investigate moisture content differences among logs and mineral soil, the moisture content of these substrates was gravimetrically determined at RS once a month from June to September 1991. Substrate samples for this analysis were collected from the top 1- to 5-cm layer from 5 to 10 randomly selected seedling plots per substrate type per stand.

Data analysis

Clone individuals and populations

Simple linear regression ($p \le 0.05$) was used to test relationships between average clone (three to nine clones per stand) or clone population (three plots per stand) characteristics and the corresponding stand density indices ($n = 9$ stands for the individual clone study and 10 stands for the population study). Natural log and square root transformations were used to normalize data when analyses of residuals indicated this was necessary. Regression analysis was also used to develop the following equation to predict total stem biomass per square metre from stem length data:

[1]   ln stem biomass $= \exp[0.208 + 0.03 \cdot$ stem length$]$

where $r = 0.88$, $R^2 = 0.7766$, $n = 78$, and SE of estimate $= 0.825$.

In excavating the salal clones, we identified three general clone types (described in Results). We used one-way ANOVA ($p \le 0.05$) to compare means of clone characteristics for the three types as well as to test differences in mean population characteristics (rhizome biomass and density, stem biomass and density, and total biomass) related to stand treatment (clearcut, thinned, or unthinned). ANOVA of nested designs was used to determine percentage of variability associated with stand treatment.

Seedling study

The following parameters were measured in the seedling study: (i) seedling emergence (maximum number of seedlings counted in a plot during the first growing season), (ii) seedling survival (number of seedlings remaining at the end of the first or second growing season divided by emergence), and (iii) seedling to seed ratios (number of established seedlings at the end of the second growing season divided by number of seeds sown (400)). Data for all three parameters were analyzed using ANOVA ($p \le 0.05$) to test for overall effects due to substrate, stand density, and study site. Least significant difference (LSD) multiple range tests were used to compare means within these three factor groups ($p \le 0.05$). Because significant differences existed among sites, data were also analyzed separately by site and by stand. For comparisons of means within study sites and within stands, we used LSD multiple range tests, two sample t-tests, and the Wilcoxon rank sum test ($p \le 0.05$).
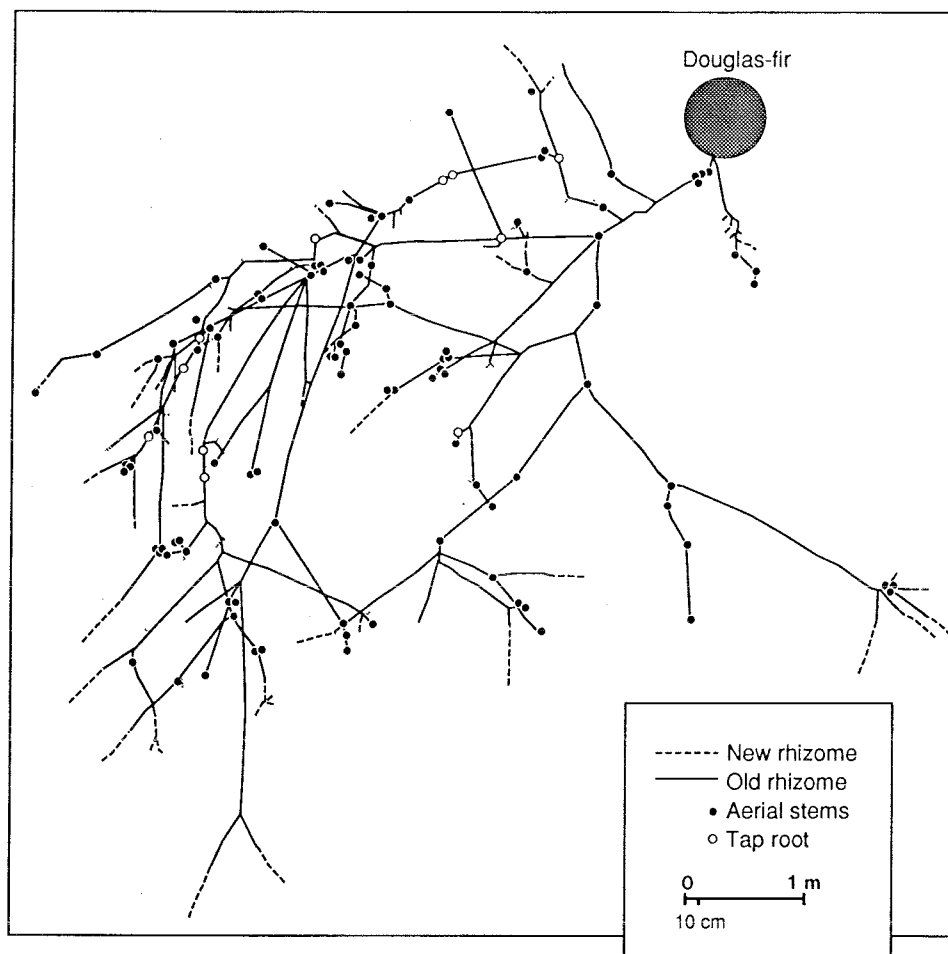
Fig. 1. Map of an excavated clone. This clone consisted of 78 ramets and 91.44 m of rhizome and was excavated in an unthinned stand (BA = 63.3 m²/ha).

Simple linear regression was used to test relationships ($p \leq 0.05$) between percent sky and the seedling survival data. The data were square root transformed when necessary.

Results

Clone study

General findings concerning clone development and architecture

At about 4 to 6 years of age, salal seedlings begin to develop into clones through rhizome production and expansion and ramet formation (Huffman 1993). Clones expand as their rhizomes grow outward along the humus — mineral soil interface. As expansion continues, large clones, consisting of many branching rhizomes connecting a number of ramets (Fig. 1), may eventually be formed. For example, we excavated clonal fragments with up to 218 m total rhizome length and 293 ramets and that covered an area of approximately 29 m². Clone development may also occur from rhizome cuttings (Messier 1992; D.W. Huffman, unpublished data) in as few as 1−2 years.

Approximately 75% of all rhizomes were found at shallow (less than 10 cm) soil depths and the remainder at depths of up to 50 cm. It was not uncommon for individual rhizomes to range in depth from 0 to 50 cm below ground. Typically, rhizomes branched at 45° to the direction of growth of the parent rhizome, and new rhizome initiation apparently was

apically controlled. Ramets are formed sympodially; formation occurs when rhizomes turn upward and produce new aerial stems (Fig. 2). That this process may take more than 1 year was evidenced by excavation of rhizome modules that proximally were dark brown, well-suberized, and woody but distally had current-growth characteristics. In addition, the longest current-season rhizome extension we measured was 94 cm, while 6% of all rhizomes (current and previous) we measured ($n > 2000$) exceeded 1 m in length (Fig. 3). The longest rhizome extension found on any clone was 282 cm, probably the result of 3 or more years of development. In addition to the sympodial development, new ramets are also produced along rhizomes between existing ramets. On clonal fragments, we found stems that were up to 25 years old and 3 m in length (very old stems tended to be decumbent). First-year stems averaged 22 cm ($\pm$ 0.75 SE) in length, whereas the longest first-year stem measured 65 cm.

The clones and clonal fragments we excavated generally could be classified into three types: type A were vigorous and rapidly expanding; type B were older and fragmented; and type C were very small, remnant fragments. Type A, which had an average current-year rhizome extension of 4.4 m and was found colonizing forest floor and soil space, occurred in all overstory stand types except the dense young stands. Ramets of type A usually had stems that were less than 10 years old. Clone origins were found for 22% of type A clones; thus, 78%
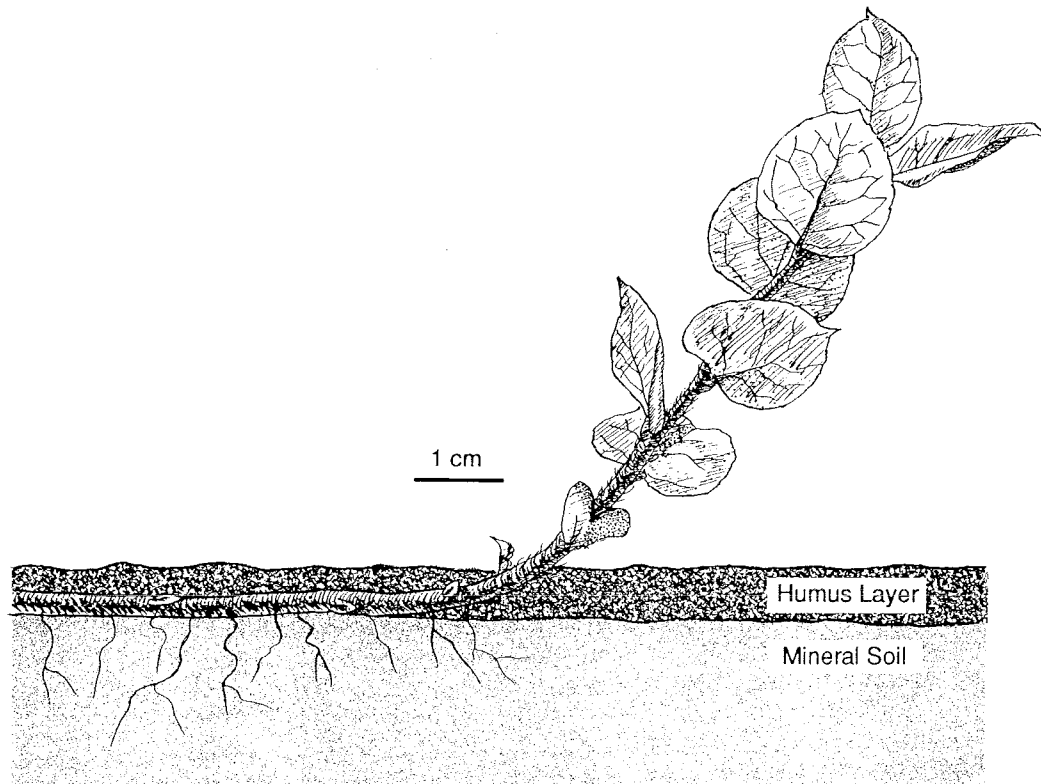
Fig. 2. Illustration of sympodial ramet formation, when a rhizome turns upward to become an aerial shoot.
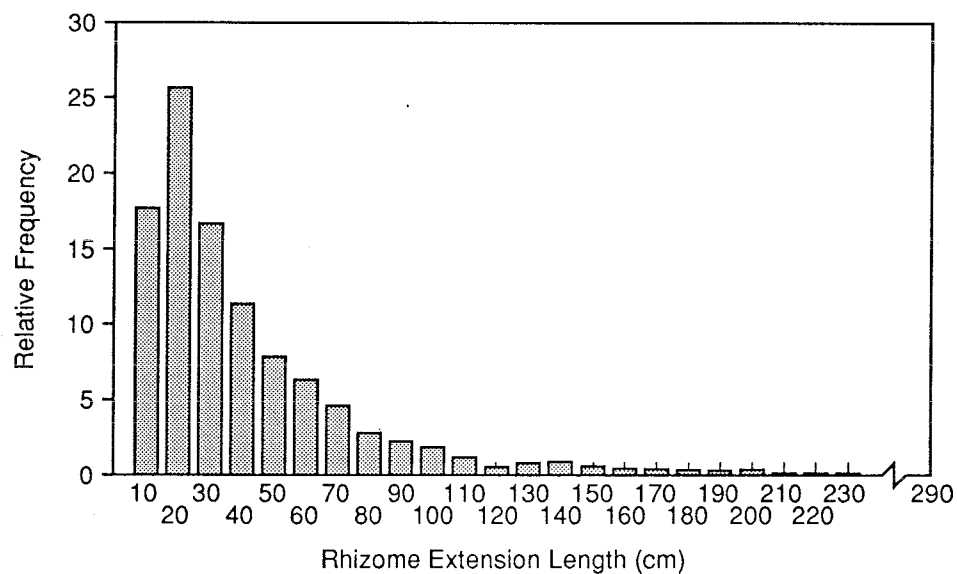

Rhizome Extension Length (cm)

Fig. 3. Relative frequency of rhizome extension lengths for all clones measured. The longest rhizome extension measured was 282 cm (not apparent in graph).

of this type were clonal fragments. Type B had ramets with stems between 10 and 25 years old in addition to young stems and were excavated from the interior of dense clumps of aerial stems. This type was not expanding rapidly (average current-year rhizome extension = 0.87 m) and appeared to be disintegrating into smaller fragments as evidenced by dead and rotten rhizomes. However, very little dead rhizome was excavated in association with any clone or clonal fragment. The type C clonal fragments were found only in very dense young Douglas-fir

stands. These were apparently fragments of clones surviving from previous stands, had no current-year rhizome extensions, and their aerial stems were no more than 2 years old. The total rhizome length of type C fragments averaged 1.57 m (Table 3).

Characteristics of these three types were statistically different (Table 3). However, some clonal fragments we excavated had both type A and type B characteristics. Four of the 15 class B clones had rhizome connections to vigorous modules on the exterior of the dense aerial stem clump.

TABLE 3. Means (±SE) of morphological characteristics for clone types A, B, and C

Clone type	n	Total rhizome length (m)	No. ramets/clone	Length of current season rhizome extension (m)	Annual growth (%)	Mean rhizome modular length (cm)	Ramet density (m rhizome/ ramet)	No. stems/ramet	Max. age of aerial stems (years)
A	23	30.55(9.49)a	35.0(15.1)a	4.44(1.25)a	16.24(1.66)a	34.2(0.73)a	0.95(0.08)a	1.69(0.04)a	8
B	14	17.81(5.87)a	16.11(5.72)a	0.87(0.32)b	5.26(1.08)b	48.33(2.18)b	1.4(0.3)a	1.46(0.08)a	25
C	14	1.57(0.56)b	1.09(0.09)b	0.0(0.0)c	0.0(0.0)c	34.89(4.9)a	1.03(0.19)a	1.45(0.21)a	2

NOTE: Type A clones typically expanded across the forest floor. Type B clones were associated with dense patches of older aerial stems, and type C (remnant) clones were found under highly stocked stands of young (30- to 40-year-old) Douglas-fir. Like letters within columns denote statistically similar means at a 95% significance level.

TABLE 4. Correlation coefficients (CC), p values, and r^2 values for regressions of average individual clone characteristics on four overstory density indices ($n = 9$)

Characteristic	Basal area			Stand density index			Relative density			Percent sky		
	CC	p	r^2	CC	p	r^2	CC	p	r^2	CC	p	r^2
Total rhizome length/clone (cm)	−0.43	0.250*	0.1825	−0.868	0.002	0.7532	−0.823	0.006	0.6780	0.818	0.007	0.6693
No. ramets/clone	−0.46	0.21*	0.2136	−0.875	0.002	0.7655	−0.796	0.01	0.6349	0.814	0.007	0.6628
Length of current-season rhizome extension (m)	−0.171	0.66*	0.0294	−0.854	0.003	0.7301	−0.820	0.006	0.6726	0.840	0.005	0.7060
Annual growth (%)	0.027	0.94*	0.0007	−0.6413	0.06*	0.4113	−0.692	0.039	0.6726	0.894	0.001	0.8001

*Relationship not statistically significant at $\alpha = 0.05$.

TABLE 5. Regression equations relating salal rhizome biomass, rhizome density, and aboveground biomass to overstory stand density (basal area) and salal stem density

Equation for relationship	r^2	SE · x^*	p
Rhizome biomass per unit ground area (kg/m²)			
BA: $y = 1263.12 - 17.34x$	0.787	262.34	0.0006
SD: $\ln y = 5.53 + 0.00586x$	0.893	0.452	0.001
Rhizome density per unit ground area (m/m²)			
BA: $\ln y = 9.28 - 0.032x$	0.813	0.448	0.0004
SD: $\ln y = 7.29 + 0.00764x$	0.945	0.339	0.00004
Aboveground biomass per unit ground area (kg/m²)			
BA: $\ln y = 7.01 - 0.018x$	0.630	0.402	0.006

NOTE: BA is the basal area (m²/ha). This index is presented due to its ease of measurement. SD is the salal stem density per unit ground area (no. of stems/m²).
*SE · x, standard error of the estimate.

Effects of overstory density on clonal fragments

Overstory stand density affected vegetative expansion, clonal fragment size, and architecture. Expansion rates (annual growth percent, i.e., the length of a clone's current-year rhizome extension divided by the sum length of all live rhizome lengths formed previously, and length of current-year rhizome extension) were significantly correlated with all overstory stand density indices except BA (Table 4). Mean annual growth ranged from 23.7% in an open stand (30% sky) to 0.0% in the dense young stands (1.2−1.7% sky). In older dense stands (8.4−12.6% sky), mean annual growth was 11.6−18.3%.

The relationship between salal clonal fragment size and overstory density was also significant. Total rhizome length and number of ramets per clonal fragment were significantly ($p \leq$ 0.01) and negatively correlated with RD and SDI and positively correlated with percent sky (Table 4), but there was no significant correlation between these parameters and BA. Mean total rhizome length per clonal fragment ranged from 102 m in an open stand (SDI = 142) to 0.89 m in a dense young stand (SDI = 398). Mean number of ramets per clonal fragment in these two stands were 124 and 1, respectively.

Measurements of clonal architecture (number of aerial stems per ramet, ramet density as metres of rhizome per ramet, and average length of rhizome modules) generally were not correlated with overstory density indices (Table 2). The only significant correlations we found were between number of aerial stems per ramet and the indices RD ($p = 0.028$) and percent sky ($p = 0.012$).

Effects of overstory density on salal populations

As with populations of other clonal species studied by Kurmis and Sucoff (1989) and Tappeiner et al. (1991), the age and size distribution of salal aerial stems apparently is unrelated to variations in overstory stand density (Fig. 4). Although the greatest range of salal stem ages was found beneath unthinned overstories, our findings indicate that clones and clonal fragments coalesce to produce dense uneven-age populations of aerial stems regardless of overstory stand density.

Salal stem density, aboveground biomass, rhizome density, rhizome biomass, and the ratio of aboveground biomass to rhi-
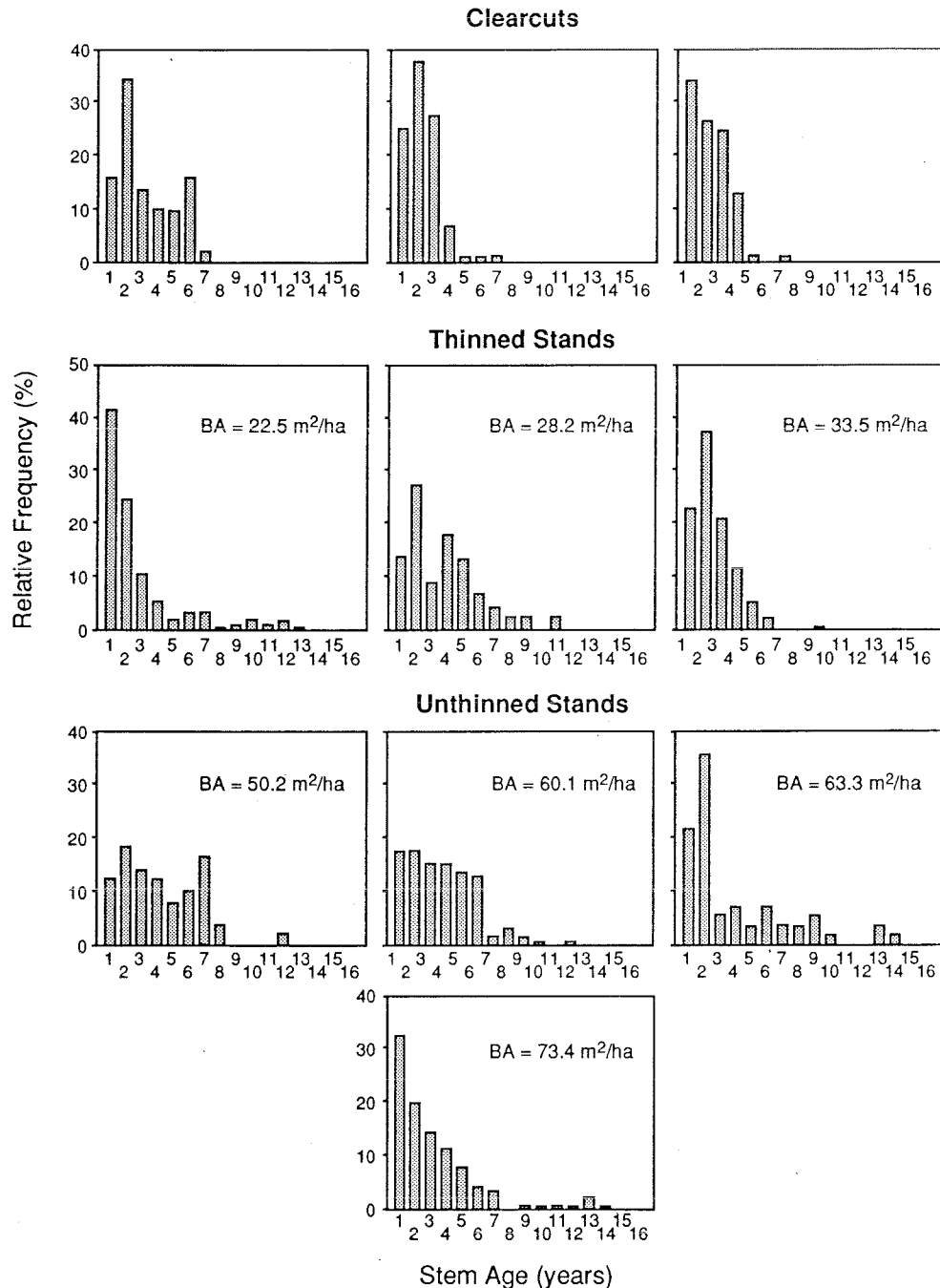
Clearcuts

Thinned Stands

Unthinned Stands

Relative Frequency (%)

BA = 22.5 m²/ha

BA = 28.2 m²/ha

BA = 33.5 m²/ha

BA = 50.2 m²/ha

BA = 60.1 m²/ha

BA = 63.3 m²/ha

BA = 73.4 m²/ha

Stem Age (years)

FIG. 4. Relative frequency of salal aerial stem ages in clearcuts (1−8 years old) and in thinned and unthinned (both 60−80 years old) Douglas-fir stands used in clone population study.

zome biomass were all significantly ($p \leq 0.01$) and negatively correlated with overstory stand density indices. Relationships of rhizome biomass, rhizome density, and aboveground biomass with BA and salal stem density are presented in Table 5; these population characteristics were also significantly correlated with RD, SDI, and percent sky (data not shown, but see Huffman 1993).

Salal population characteristics varied significantly ($p \leq 0.05$) among general overstory treatments (clearcut, thinned, unthinned) (Fig. 5). Clearcuts had significantly greater rhizome biomass, total rhizome density, and stem density than thinned stands and unthinned stands. No differences were found between clearcut and thinned stand means for current rhizome density, aerial stem biomass, or total biomass, but the means for these

two overstory types were significantly greater than those for unthinned stands (Fig. 5).

Although there were significant differences among stands within each general overstory treatment, from 79 to 86% of the variation in rhizome biomass, rhizome density, and stem density and from 48 to 72% of the variation in total biomass and new rhizome density were associated with stand type.

Seedling establishment

Emergence

Seedling emergence began in early April 1991. At all three study sites, seedlings emerged earliest in the clearcuts. Emergence peaked in mid-July, 1991; in the months that followed, much seedling mortality occurred.
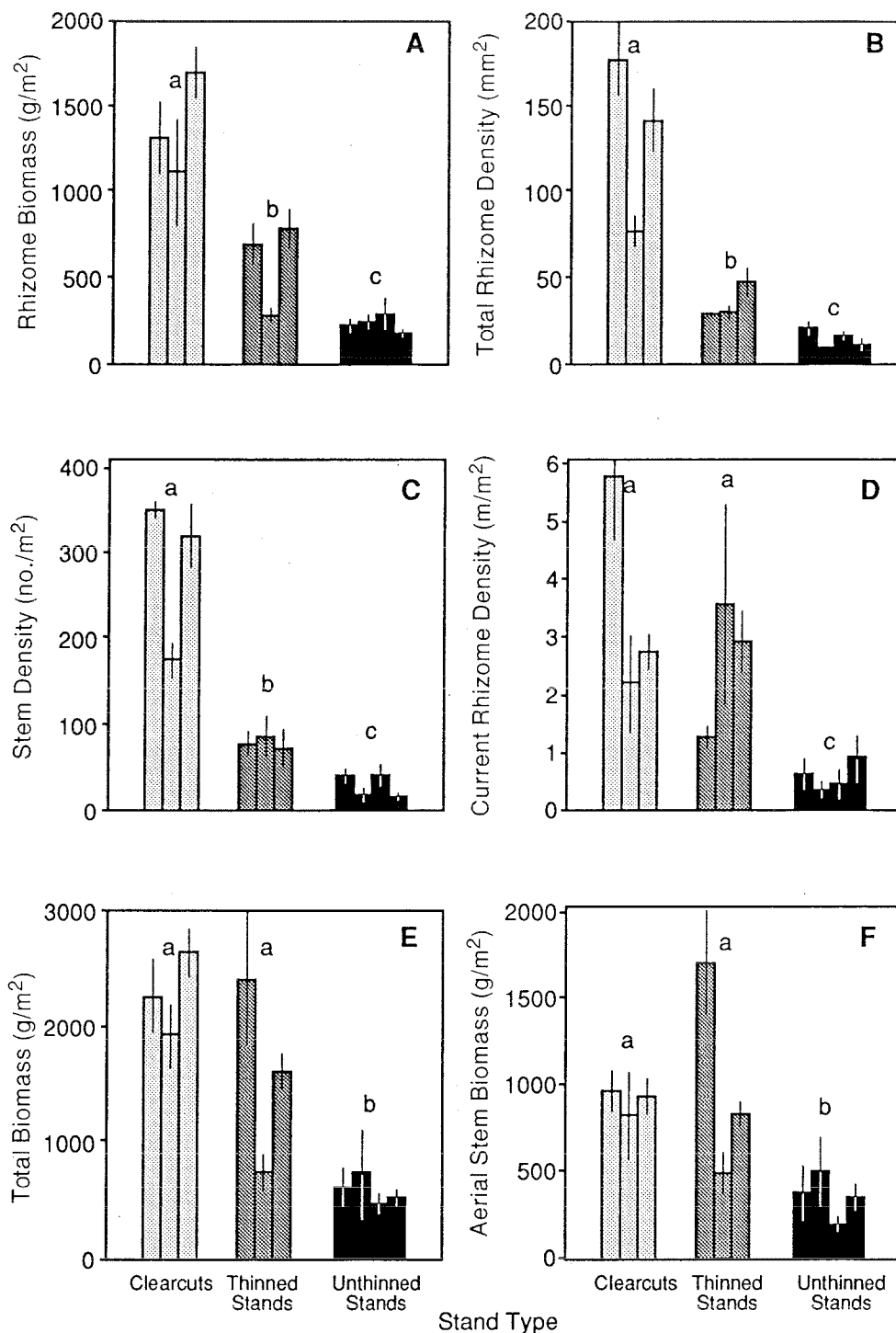
FIG. 5. Means of salal population characteristics in clearcuts, thinned stands, and unthinned stands. Like letters among stand types denote statistically similar means at a 95% significance level. Each bar represents the mean (+ SE) for three plots in an individual stand.

Significant ($p \leq 0.05$) differences in total emergence (maximum number of seedlings counted in a plot) were found among study sites, overstory treatments, and substrates (Table 6). The RS site had significantly less emergence than CP or CS; emergence at the latter two sites was not statistically different. There was no significant difference between emergence in thinned and unthinned stands; however, both of these overstory treatments had significantly higher emergence than clearcuts.

On average, from two to three times more seedlings emerged on logs than on undistrubed forest floor and mineral soil.

First-year survival

In October 1991 (the end of the first growing season) overall mean seedling survival was 14.1%. The tallest seedlings at this time were 4.4 cm in height. As with emergence, significant differences ($p \leq 0.05$) in 1st-year survival rates were
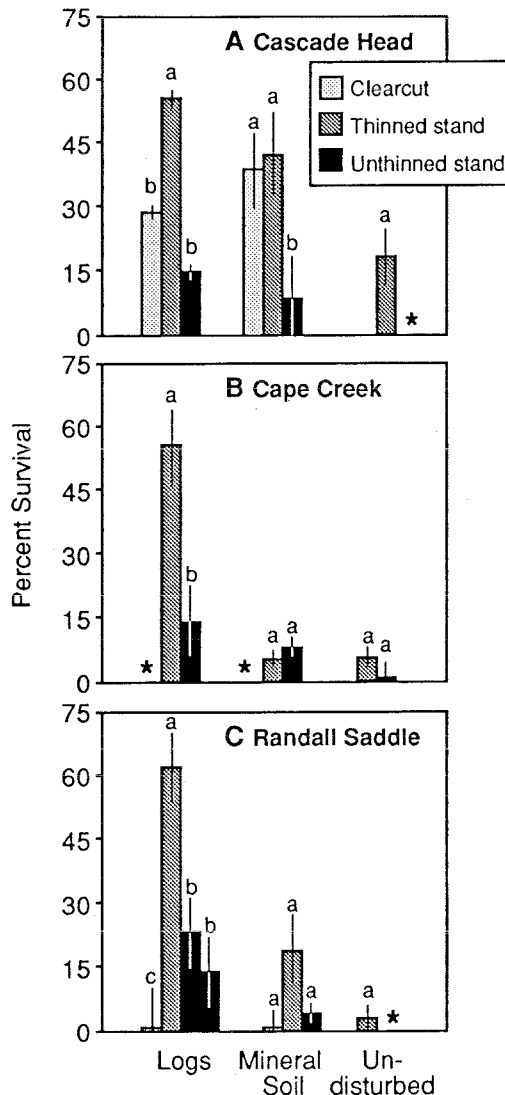
FIG. 6. Mean percent 1st-year survival of seedlings, by site, substrate, and overstory density; vertical bars indicate one standard error of the mean. Like letters within substrate groups denote statistically similar means at a 95% significance level. There were no undisturbed plots in clearcuts. *, no survival.
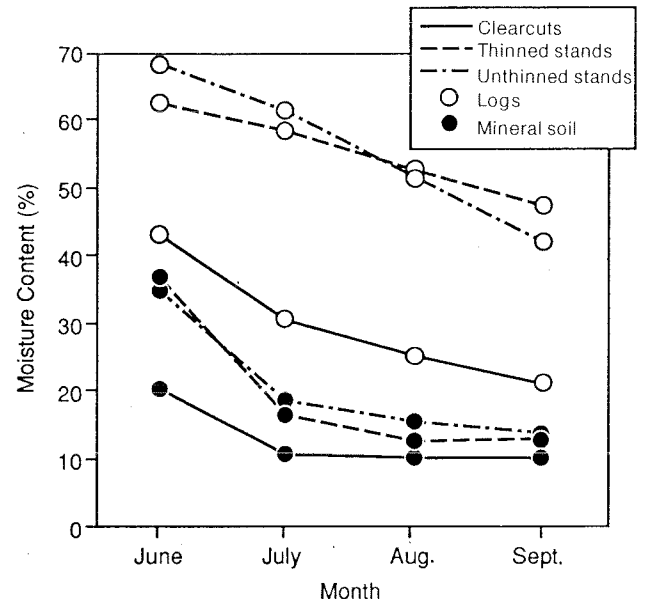

FIG. 7. Moisture content, in percentage by weight, of logs and mineral soil in clearcuts, thinned stands, and unthinned stands at Randall Saddle during the 1991 growing season.

observed among study sites, overstory treatments, and substrates. Mean 1st-year survival was significantly greater at CS (23.6%) than at CP or RS; survival rates for the latter two sites were not statistically different (8.1 and 10.5%, respectively). Across study sites, mean 1st-year survival differed significantly by stand type; it was greatest in thinned stands (30.1%), less in unthinned stands (8.0%), and least in clearcuts (4.3%). Across sites and overstory treatments, significantly higher survival occurred on logs (25.4%) than on mineral soil (14.3%); undisturbed forest floor consistently had the lowest survival (2.6%). When study sites were analyzed separately, 1st-year survival in thinned stands and on logs consistently was significantly higher than in other overstory treatments or on other substrates (Fig. 6).

A significant ($p \leq 0.009$; $r^2 = 0.34-0.60$) correlation was found between percent sky and 1st-year seedling survival on logs, both for the three sites combined and for each site

individually. This relationship was not as strong for other substrates. For example, at CP, there was no significant correlation between survival on mineral soil or undisturbed forest floor and percent sky ($p = 0.25-0.90$). Logs were also found to have a higher moisture content by weight than mineral soil throughout the growing season (Fig. 7).

Second-year survival and height

The seedling population declined through the second growing season, and in September 1992 across all study sites, overstory treatments, and substrates, an average of 4.47% of the emerged seedlings remained. Evidence from previous research indicates that salal seeds lack innate dormancy and are transient in forest floor seed banks (McGee 1988; J.C. Zasada, unpublished data). This information, plus easily identifiable features of older seedlings (i.e., true leaf morphology), led us to assume that no new seedlings were counted during the second growing season. All factors (study site, overstory treatment, and substrate type) significantly ($p \leq 0.05$) affected survival (Table 6). Average 2nd-year survival was not statistically different at RS and CS but was significantly lower at CP. Thinned stands had significantly greater survival than either unthinned stands or clearcuts, and mean survival on logs was significantly greater than on mineral soil, which in turn was significantly greater than mean survival on undisturbed forest floor (here, survival was not significantly different from zero).

At the end of the second growing season, seedling heights ranged from 0.2 cm, in an unthinned stand at CP, to 20 cm in a thinned stand at RS. The average seedling height across all sites, overstory treatments, and substrates was 2.4 cm (±0.16 SE). Mean seedling height was significantly ($p \leq 0.05$) greater in thinned stands (2.51 cm) than in unthinned stands (1.89 cm). Too few seedlings survived in clearcuts for comparison; however, those surviving on mineral soil in the CS clearcut were exeptionally tall, averaging 4.18 cm. Also, no differences in seedling heights were found among substrate

and (iii) the ability of salal to tolerate conditions of relatively low light. Salal clones, clonal fragments, and populations may expand and increase in biomass following heavy thinning or clearcutting of forests. Dense salal patches may expand an average of 311 cm/year, and up to 582 cm/year, under these conditions. Apparently, after clearcut logging, salal reoccupies a site through vigorous rhizome expansion and aerial stem production coming from surviving rhizomes. Rhizome systems of individual clones may expand up to 23% annually after thinning. Expansion and probable coalescence of clones leads to dense patches (cover ≥ 90%). Because of their uneven-aged nature, their shade tolerance, and the longevity of their aerial stems, these patches may persist. They may provide habitat and forage for some wildlife species, and yet they will also shade out herbaceous plants and prevent the natural establishment of tree and shrub seedlings in the understory.

Thinned stands retaining large amounts of downed and rotting wood provide conditions suitable for salal regeneration from seed. Up to 25% of the seed rain on logs may emerge, and up to 3% may produce seedlings that survive for at least 2 years. Seedlings, however, appear to grow slowly and apparently do not begin to expand vegetatively for from 4 to 6 years; this suggests that colonization is most rapidly accomplished through the expansion of rhizome systems. Thus, if salal clones are not present in a stand, the potential for rapid colonization is greatly reduced.

Dense overstories appear to constrain seedling establishment, and when overstory density is greater than 360 SDI, rhizome growth is also hindered. At this overstory density, clonal fragments are much reduced in size. These smaller clones continue to subsist, however, and it is not clear how rapidly they may respond to disturbances of the overstory.

Acknowledgment

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